Genomic dairy cattle breeding: risks and opportunities for cow welfare

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Abstract

The aim of this paper is to discuss the potential consequences of modern dairy cattle breeding for the welfare of dairy cows. The paper focuses on so-called genomic selection, which deploys thousands of genetic markers to estimate breeding values. The discussion should help to structure the thoughts of breeders and other stakeholders on how to best make use of genomic breeding in the future. Intensive breeding has played a major role in securing dramatic increases in milk yield since the Second World War. Until recently, the main focus in dairy cattle breeding was on production traits, but during the past couple of decades more emphasis has been placed on a few rough, but useful, measures of traits relevant to cow welfare, including calving ease score and 'clinical disease or not'; the aim being to counteract the unfavourable genetic association with production traits. However, unfavourable genetic trends for metabolic, reproductive, claw and leg diseases indicate that these attempts have been insufficient. Today, novel genome-wide sequencing techniques are revolutionising dairy cattle breeding; these enable genetic changes to occur at least twice as rapidly as previously. While these new genomic tools are especially useful for traits relating to animal welfare that are difficult to improve using traditional breeding tools, they may also facilitate breeding schemes with reduced generation intervals carrying a higher risk of unwanted side-effects on animal welfare. In this paper, a number of potential risks are discussed, including detrimental genetic trends for non-measured welfare traits, the increased chance of spreading unfavourable mutations, reduced sharing of information arising from concerns over patents, and an increased monopoly within dairy cattle breeding that may make it less accountable to the concern of private farmers for the welfare of their animals. It is argued that there is a need to mobilise a wide range of stakeholders to monitor developments and maintain pressure on breeding companies so that they are aware of the need to take precautionary measures to avoid negative effects on animal welfare and to invest in breeding for increased animal welfare. Researchers are encouraged to further investigate the long-term effects of various breeding schemes that rely on genomic breeding values.

Keywords: *animal welfare, dairy cattle, genetic progress, genomic selection, inbreeding, side-effects*

Introduction

Selective breeding is a powerful tool that can be used over time to substantially change animal populations to suit human goals. It can modify any heritable trait, including traits which may affect the welfare of the animal. In fact, such traits (which, in this paper, we refer to as 'welfare traits') can be affected even when they are not considered directly in a breeding scheme, due to correlated effects. Important welfare traits in dairy cattle include those affecting disease resistance, survival, calving ease and the ability to perform various forms of 'natural' behaviour. The main aim of cattle breeding has always been to maximise profits for the farmer. This has often resulted in production traits receiving the highest emphasis in selection indices (Miglior *et al* 2005). However, of late, there has been an increasing focus on so-called functional traits, including welfare traits. Before looking at the impact of genomic selection on cow welfare we shall try briefly to summarise the main impacts that breeding has had on dairy cattle in the past few decades.

Genetic trends in welfare traits: an incomplete picture and mixed signs

The deterioration of mastitis resistance in the international Holstein breed during the 1980s and 1990s is an example of an undesirable side-effect of the high emphasis on production traits in selection decisions. The deterioration can be explained by a negative genetic correlation between clinical mastitis resistance and production traits of approximately –0.4 (eg Heringstad *et al* 2000). To date, only the Nordic countries included direct information about clinical mastitis in their selection index, while other countries had only indirect information via somatic cell score and udder conformation. However, the lack of focus on clinical mastitis in these other countries also contributed to the negative genetic trend in Nordic countries, since mainly foreign bull sires were used in the Nordic region. In recent years, the negative genetic trend has been broken, and mastitis resistance has improved slightly in the Nordic countries (Danish Cattle Federation 2008). This illustrates

the fact that, via breeding, it is possible to improve a welfare trait while simultaneously improving production.

Mastitis resistance is just one of several significant traits affecting dairy cattle welfare. Unfavourable genetic trends have been documented for metabolic, reproductive, claw and leg diseases in Danish and Swedish Holsteins as well as in Red cattle (Johansson *et al* 2008). Direct measures of clinical disease traits are not systematically recorded outside the Nordic countries. Genetic trends in non-Nordic Holstein populations are therefore unknown, but they are expected to be more unfavourable than they are in Nordic countries due to the lack of direct selection emphasis on these traits.

Generally, there tends to be an unfavourable genetic correlation between production and welfare traits (eg Rauw *et al* 1998). Hence, welfare traits that are not recorded systematically (referred to hereafter as 'non-measured' traits) may well be under greater negative pressure than udder health. Although the selection emphasis on cow survival, somatic cell score and other functional traits in many official selection indices ought to counterbalance the negative side-effects of increased production, suboptimal selection and mating decisions are likely to have caused unfavourable genetic trends for welfare traits.

Interbull (2009) indicates that the following welfare traits are currently being systematically recorded and evaluated in various countries: i) cow survival (or longevity); ii) calving ease; iii) calf survival until 24 h after birth; and iv) clinical mastitis and most of the common reproductive, metabolic and claw and leg diseases (only Nordic countries). Furthermore, selection against known genetic defects such as Complex Vertebral Malformation (CVM) and Bovine Leukocyte Adhesion Deficiency (BLAD) is carried out. Desirable temperament for farmer handling (especially in connection with milking) is also widely considered, but it is not known how this correlates with the ability of the cow to perform 'natural' behaviour that is of relevance to its welfare.

The measures mentioned above are useful, but also quite rough, and are unlikely to capture all relevant genetic variation with respect to cow welfare. For instance, cow survival is not a clean measure of the cow's own ability to survive since it reflects both spontaneous deaths and management decisions to cull cows. Also, diseases and mortality between day one and first calving are ignored. Thus, the picture of genetic trends with respect to welfare traits is incomplete, especially where cattle populations outside the Nordic countries are concerned, and there is reason to believe that present day dairy cattle breeding could have negative effects on the welfare of future generations of dairy cattle.

Genomic selection is revolutionising dairy cattle breeding

Genomic selection (Figure 1) is a new technology in which breeding values are predicted from genome-wide markers in the form of SNP (referred to as 'genomic BV' hereafter). With this technology, the total breeding value of an animal is, so to speak, sliced into thousands of small black boxes instead of just one big black box.

Genomic BV is conceptually simple to calculate. First, the entire genome is divided into small chromosome segments by dense markers (eg Illumina 50K BeadChip; Illumina 2009). Second, the effects of each chromosome segment are estimated simultaneously. Finally, the genomic BV equals the sum of all chromosome segment effects (Meuwissen *et al* 2001). The chromosome segment effects can be estimated for a group of animals (ie a reference population); and for any remaining animal, only a blood or tissue sample is needed to determine its genomic BV (Figure 1). The chromosome segment effects apply to all animals in the population in which they were estimated, because markers are in linkage disequilibrium with the causal gene that they bracket.

High levels of accuracy of breeding values are essential for achieving genetic progress. The accuracy of genomic BV increases when the size of the reference population increases, when the reference population represents as much of the relevant genetic variation in the population as possible, when selection candidates are closely related to the reference population, and with better statistical models. More informative marker maps also increase accuracy, although the increase here is marginal when the marker density is already high (ie 50,000 markers for within-breed selection).

More than 10 of the largest dairy countries already, or will soon, publish and use genomic BV in selection decisions (eg Loberg & Dürr 2009). Initially, it appears that genomic BV will be available for traits that have been considered previously. It is not known at present, however, exactly what consequences the availability of accurate genomic BV will have for the design of breeding schemes, except that more selection emphasis will be directed on young animals.

In Nordic countries, genomic BV is presently used to intensify the pre-selection of young bulls to be progeny-tested. Furthermore, semen collection is initiated earlier for promising bulls for which progeny information is expected and up to 10,000 semen doses from each of the most promising young bulls, based on genomic BV, are used right away (currently 12 such Holstein bulls are advertised), whilst 20% of the waiting bulls with the lowest genomic BV are culled (Lars Nielsen, VikingGenetics personal communication 2009). In 2009, 33% fewer young bulls were tested than during the previous year, but the screening is expected to be much more accurate than the previous screening, which was based primarily on the average breeding values of parents.

The use of young bulls with high genomic BV is tempting, even though the accuracy of breeding values here is only approximately 70% (Su *et al* 2010; this compares with more than 90% after the progeny group-test). This is the case because deterministic (Schaeffer 2008) and stochastic (Sørensen & Sørensen 2009) simulations of breeding schemes indicate that the use of young bulls with high genomic BV will result in greater total genetic progress per year. Also, substantial costs can be saved (König *et al* 2009). Hence, future selection may not wait for progeny results but, instead, make considerable use of bulls with high genomic BV regardless of age.

Figure 1

Illustration of genomic selection.
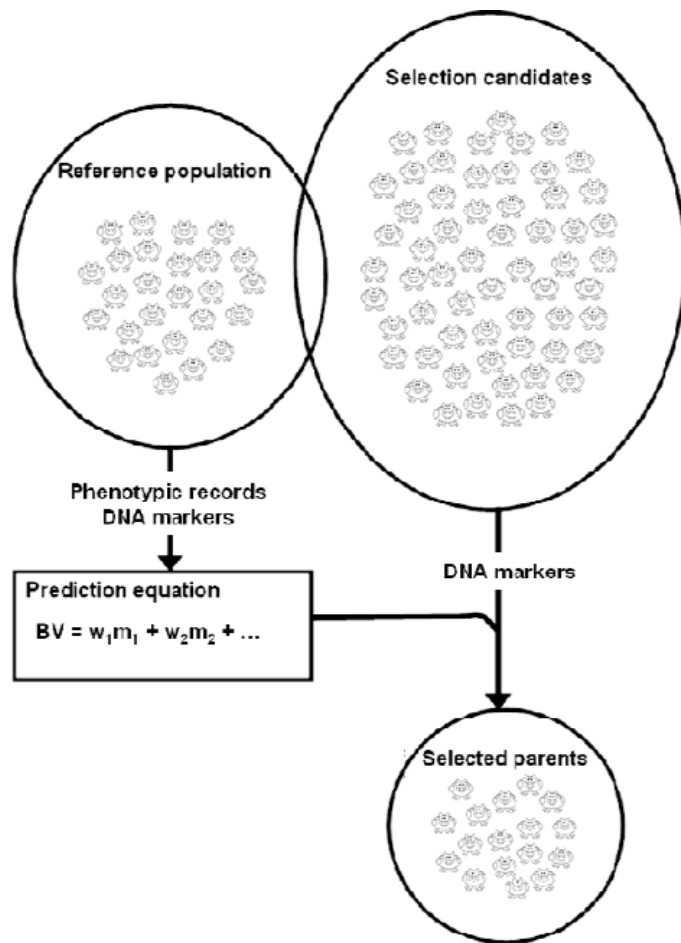
An extreme breeding scheme based on genomic BV — and one that may be both possible and attractive in the future — is 'laboratory breeding'. This has also been called 'velogenetics' or 'whizzogenetics' (Georges & Massey 1991; Haley & Visscher 1998). Here, rapid breeding cycles based on advanced embryo technology are run in the laboratory, thereby reducing the generation interval to a few months. However, laboratory breeding is not realistic in the near future, because the necessary *in vitro* culturing, fertilisation and growth of cells still need to be developed. Furthermore, it is currently difficult and costly to SNP genotype embryos, and problems with large calves resulting from ovum pick-up (eg Feugang *et al* 2009) need to be resolved. Finally, only a few generations can be developed in the laboratory before phenotypes are needed to re-estimate marker effects, because the accuracy of these effects decreases as the distance between selection candidates and animals with phenotypes increases.

Researchers and the industry were quick both to develop systems for accurate prediction of genomic BV, and to start using these to enhance breeding schemes after dense marker-maps became available in 2008. While the animal breeding community is excited about the potential of genomic selection in facilitating genetic progress, it remains uncertain which strategy using genomic BV will be applied and how this will affect animal welfare.

The aim of this paper is to discuss the potential impact of modern dairy cattle breeding using genomic BV on cow welfare. We will try to spell out what we see as the opportunities and risks for animal welfare. Thus, our aim is not so much to predict what is going to happen, but rather to help structure the thoughts that breeders and other stakeholders may have about how best to use genomic BV in the future. We hope that our suggestions and warnings will be useful in ensuring that the technology is used in a way that benefits the welfare of future generations of dairy cattle.

The next section of the paper is based on a review of the relevant literature, basic quantitative genetic theory, and information from persons responsible for the implementation of genomic selection in Nordic Holsteins.

Opportunities of genomic selection

In a number of ways, the genomic BV-based breeding of dairy cattle may result in improved cow welfare. The

improvements here mainly have to do with the fact that the new technology allows for earlier selection.

Faster genetic progress for all evaluated traits, especially evaluated welfare traits

The animal breeding community is excited about genomic BV because high levels of accuracy (ie a strong correlation between true and predicted BV) can be achieved for genomic BV at an early stage in the animals' lives. In fact, the genomic BV can be predicted as soon as DNA can be collected from the animal, which in principle could be done at the embryonic stage. Meuwissen *et al* (2001) indicated in a simulation study that the accuracy of genomic BV could be over 80%. Practical results indicate that the accuracy of genomic BV ranges between 50–84% for all traits considered in the Nordic countries, and between 56–66% for welfare traits; these figures are substantially higher than the average of parents breeding values (Su *et al* 2010). Accuracies for welfare traits are similar to production traits when chromosome effects are estimated using an ample number of records. Relatively higher accuracy will also be seen at the time of selection for traits measured late in the animals' life which could favour robust cows being able to produce milk for a longer time. The relatively higher accuracy for welfare traits with genomic selection combined with a reduced generation interval means that relatively higher levels of genetic progress for welfare traits can be expected for an unchanged breeding goal and recording strategy.

Figure 2 shows how the accuracy of genomic BV, when it is blended with information from traditional breeding values, is much higher than the accuracy of traditional breeding values for young animals. The disparity decreases as the animal gets older and more information is received about its Mendelian sampling term via its own, or progeny, records. Genetic progress is proportional to the accuracy divided by the generation interval, and therefore the genetic progress per year achieved by traditional selection is expected to be more than doubled by genomic selection (Schaeffer 2008; Sørensen & Sørensen 2009). When animals produce many progeny at an early age, as is likely to happen in genomic selection schemes, the accuracy of genomic BV blended with information from traditional breeding values would increase faster than the rate indicated in Figure 2, which is based on generation intervals in current progeny testing schemes.

Less inbreeding at unchanged selection intensities

The use of genomic BV, rather than traditional breeding values, results in less inbreeding if the same selection intensities are maintained. This happens because breeding based on traditional breeding values puts more emphasis on parent information than genomic BV (Daetwyler *et al* 2007), especially for traits with low heritability. Lower levels of inbreeding result in less inbreeding depression, less lethal recessive alleles being expressed, less variation in response to selection, greater diversity and greater opportunity to fix genetic problems through breeding. Hence, reduced

inbreeding is good for animal welfare. Lower levels of inbreeding depression are especially advantageous for welfare traits (Sørensen *et al* 2008).

In practice, these positive effects may be reduced as the result of a number of factors. Thus, it is likely that selection intensities for bulls will increase, because with genomic selection the need for progeny group-testing is reduced. Progeny data are no longer necessary in order to evaluate a bull's breeding value, although the progeny records of several bulls are needed for the accurate estimation of marker effects. In practice, breeding organisations have reduced the number of bulls being progeny group-tested after genomic predictions became available, at least in Denmark and Sweden. Also, some breeding organisations combine genomic BV with the average BV of parents via selection index (eg VanRaden *et al* 2008; de Roos *et al* 2009). This improves accuracy — at least, when one parent is not genotyped — but at the same time it reduces the advantage of genomic selection over traditional selection with respect to inbreeding.

More accurate selection of foreign bulls, especially for welfare traits

Foreign bull sires with no daughters in a given country can be selected more accurately for all breeding goal traits in the given country through genomic BV. This is especially true for traits that are not recorded in some countries: for example, direct health traits, traits with low across-country genetic correlations, including cow survival, and traits with low heritabilities, such as clinical mastitis, calving traits and cow survival (Interbull 2009). Thus, genomic selection is especially advantageous for welfare traits when it comes to foreign bull selection. For Holsteins, it is common to use at least 50% foreign bulls; a lower percentage is used for other breeds.

In the Nordic countries, all potential bull sires from other countries are now required to have a genomic BV before being included in the breeding programme as a bull sire. In this way it is hoped that the unfavourable genetic trend for diseases other than mastitis will be reversed or halted. Countries that do not evaluate certain traits (eg direct health traits) may use genomic prediction formulae from another country. This is expected to be better than doing nothing — at any rate, assuming a positive across-country genetic correlation between the countries and a similar genetic composition of the two national populations.

Better opportunity for genetic evaluation of traits which are expensive to measure

Relatively high levels of accuracy can be obtained for traits that are systematically recorded on a large scale, as mentioned above. Presently, genomic BVs are computed only for traits for which traditional BVs are also available, but important traits that are expensive to measure may be added in the future. It is also possible to estimate marker effects by gathering phenotypes for a representative fraction of the population and using these for genomic selection among animals without recorded phenotypes. This could be of

Figure 2

Accuracy (r_{IA}; correlation between predicted and true breeding value) of breeding values based on traditional phenotypic records only (dotted curve) and of breeding values based on both genomic and phenotypic information combined via selection index (solid curve). The accuracy is shown as a function of age for a bull receiving both 1st and 2nd crop daughters (upper), and a cow which initiates a new lactation each year from two years of age (lower). In this example, a heritability of 0.15 was assumed.
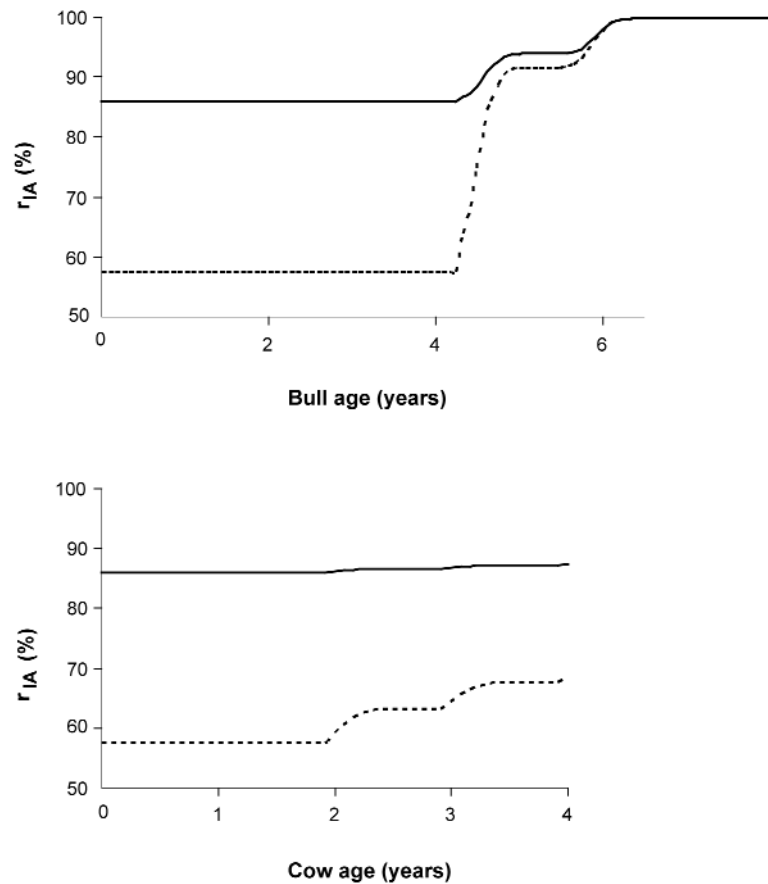
interest in connection with traits that are difficult, or expensive, to record on a large scale but economically important. With regard to welfare traits, it might, for instance, be desirable to compile more comprehensive records of certain health traits (eg bacteriological samples, severity of disease, physiological measures, and repeated records). The quantity of records needed will depend on the heritability of the trait; more records are required when heritability is low (Goddard 2009; Figure 3) and this could prevent the consideration of certain such traits for genomic selection.

Centralisation of breeding could enable closer to optimal selection and mating decisions

The introduction of genomic selection may result in the centralisation of cattle breeding programmes for a variety of reasons: (i) there are large-scale benefits in terms of smaller costs per animal to cover the investments necessary for the achievement of a given accuracy of genomic BV (a fixed number of genotypes, phenotypic records and a certain number of human work hours are required to achieve a given level of accuracy); (ii) recorded phenotypes and genotypes are required for a

fraction of the population only; (iii) increased technological know-how is required, especially if laboratory breeding takes off (even though some services such as genotyping could be outsourced) and; (iv) patents may prevent some breeders from performing genomic selection. Furthermore, it is easier to ensure optimal selection and mating decisions in a nucleus breeding scheme where there is central control over all major decisions — but this is not specific to genomic selection.

Centralisation may be instrumental in closing the gap between optimal and realised genetic progress and thereby help to improve animal welfare. Currently, there is often a considerable gap between what could be achieved and what is achieved in practice (König *et al* 2007), because suboptimal selections and mating decisions occur. If breeding becomes more centralised, it may become easier to avoid these suboptimal decisions.

The combination of small national populations in joint breeding programmes is another element of centralisation that may be stimulated by the availability of genomic BV. This is because it is easier to maintain a large reference population with larger joint populations.

Figure 3
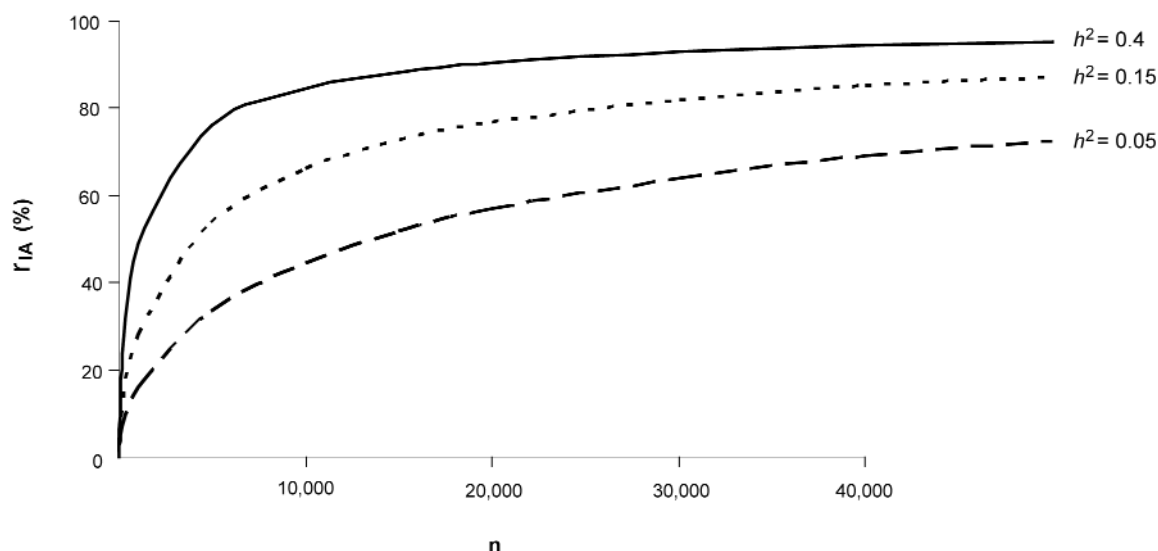
Accuracy of genomic BV (r_{IA}) as a function of number of phenotypic records (n) used to estimate marker effects for traits with heritability of 0.4 (solid curve), 0.15 (dotted curve) and 0.05 (broken curve); derived from a formula presented by Goddard (2009) that assumes normal distribution of marker effects.

This is especially important in improving the accuracy of genomic BV for traits with low heritability, including most welfare traits (Figure 3).

Risks of genomic selection

In the hands of dairy cattle breeders, genomic selection is proving to be a powerful tool. Like most new technologies this tool is, in itself, neither good nor bad: what comes out of it depends on how it is used. Used properly, genomic BV may, as described in the previous section, lead to increased dairy cattle welfare. However, there is a real danger that where vital information is missing, or in the hands of people with a narrow focus on short-profit, genomic BV will be used to speed up developments which are detrimental to animal welfare. We shall now outline a number of such potentially negative developments.

Stronger correlated selection pressure on non-measured traits may be unfavourable

The correlated response to selection for a non-measured trait is proportional to the response to selection for evaluated traits (ie traits included in the selection index) and to the genetic correlation between the non-measured trait and the selection index. Hence, with a constant negative genetic correlation between the non-measured trait and the selection index, the unfavourable genetic trend for the non-measured trait will worsen when the response to the selection of evaluated traits increases as the result of genomic selection. However, the correlation between the non-measured trait and the selection index will be less negative (or even positive) following genomic selection if the non-measured trait is positively correlated with welfare traits, because the latter receive relatively more emphasis with genomic selection due to the relatively greater increase in accuracy they undergo as compared with production traits.

Table 1 illustrates a changed correlated selection pressure with a simple example. In this example, genomic selection gives higher total economic progress and higher progress for the two welfare traits (health A and B) when all traits are measured. However, it also gives a greater decrease in genetic level for health B than one obtains in a traditional breeding scheme when this trait is not measured.

Furthermore, some non-measured traits, such as health and fertility, are subject to natural selection besides the correlated influence of traits included in the selection index. If natural selection acts on characteristics expressed late in life (eg during lactation), it will be weaker when generation intervals are shortened, as is the case in genomic selection and, particularly, laboratory breeding. In most countries, important welfare traits are not measured, and so genomic selection could, at least for the time being, be worse for animal welfare than traditional selection.

Higher risk of spreading unfavourable mutations

Genomic BV does not capture the effect of new non-recurrent mutations in selection candidates without phenotypic information (relating to self or progeny). The reason for this is that phenotypic information from animals carrying the new mutation is needed to estimate the effect of the new mutation. If selection and mating decisions are made before there is phenotypic information available from progeny, or the animal itself, it becomes impossible to

Table 1   Expected genetic progress (expressed in trait units per 0.01 × σ$_p$[1]) for four different breeding strategies that differ only in respect of information sources considered for genetic evaluation[2].

Strategy	Production	Health A	Health B
(T1) Traditional; all traits measured	25.5	0.32	−0.65
(T2) Traditional; health B not measured	27.5	0.43	−1.66
(G1) Genomic; all traits measured	34.8	2.59	0.44
(G2) Genomic; health B not measured	35.5	2.50	−1.82

[1] Phenotypic standard deviation.
[2] Genetic progress was simulated using selection index and truncation selection as in Rutten *et al* (2002); Genomic breeding strategies (G1 and G2) were implemented as in Dekkers (2007); Economic values in the breeding goal were always 2:2:1 (per σ$_p$; order of traits: production, health A, health B); Heritabilities were 0.35, 0.05 and 0.05; Genetic correlations were −0.2 between production and health traits and 0.2 between the two health traits; Accuracy of markers as predictor of genetic component was 0.7 for all available traits.

estimate the effect of a new mutation. Hence, in practice, a new mutation will not affect the genomic BV. On the other hand, a mutation with significant negative or positive effects, carried by a bull with many progeny, will affect the breeding value of this bull.

This has two important implications. First, favourable mutations will be less likely to be captured with genomic selection. In order to be picked up, the mutation must be carried by a selection candidate with otherwise superior genetic effects. Cows could introduce new favourable mutations, but with faster female generation cycles (achieved through the use of heifers for embryonic transfer to produce bull dams), the chance of picking up favourable mutations via the female side is also reduced. This is expected to negatively affect long-term genetic improvement in all traits (Hill 1982).

Secondly, certain unfavourable mutations may be more easily spread in the population and seriously reduce animal welfare. Lethal mutations occurring early in life are unlikely to be spread more easily in breeding schemes that rely on genomic selection than they are in traditional progeny test breeding schemes, except when fast generation cycles are performed in the laboratory. However, non-lethal mutations of genes controlling physiology during lactation or the cow's ability to calve easily would most probably be spread more easily in genomic selection breeding schemes, because the relevant phenotypes (eg metabolic disorders) will not have been expressed at the time of selection and therefore will have been subjected to neither direct, indirect nor natural selection. For bull selection, it could take two generations before such mutations are seen, and there is therefore a real risk that they would be spread significantly in genomic selection breeding schemes before abnormalities resulting in animal suffering are discovered. In faster generation cycles based on laboratory breeding, this risk will increase.

So far as we have been able to determine, the effect of mutations in genomic selection breeding schemes has not yet been investigated. More research in this area — for example, stochastic simulations of genomic breeding schemes that account for realistic long-term effects of mutations — is desirable.

Risks of centralisation, monopoly and reduced sharing of information

Genomic selection may encourage the centralisation of breeding programmes and selection decisions, as mentioned above. This means that breeds, countries, regions or companies with more animals will have an advantage over smaller units, and that breeding programmes for some smaller units may not be competitive. This could have negative implications for animal welfare.

Thus, the dominance of the Holstein breed may become more pronounced, and opportunities for cross-breeding may deteriorate further. Cross-breeding is known to positively affect welfare traits such as health and survival ability (Sørensen *et al* 2008), so less cross-breeding would have a negative impact on welfare traits. Furthermore, more pronounced domination of the Holstein breed would decrease genetic diversity and limit opportunities for adaptation to new production circumstances in the future.

Some countries — developing countries or countries with few dairy cows, for example — may not have sufficient resources to successfully implement genomic selection. Such countries would either merge their breeding programme with programmes for larger populations, implement a less ambitious genomic selection scheme (eg with a smaller reference population, or with less frequent updates of marker effects), or become heavily dependent on objective international comparisons, such as those obtainable via Interbull. Such comparisons may become problem-

atic in the near future for two reasons. First, international genetic evaluations are less valuable for countries where genomic selection takes place. These countries may therefore be unwilling to pay for a service that mainly benefits others, and be reluctant to prioritise the necessary research and development in this area. Second, pre-selection due to genomic BV is difficult to account for and could cause substantial bias in international evaluations. For both of these reasons, the usefulness of international evaluations will be reduced, and it could become more difficult for some countries to select foreign bulls for their own production circumstances.

Increased competition and concerns over patents may result in less sharing of genotypic and phenotypic data among genetic evaluation centres, resulting in lower accuracy of genomic BV and less genetic progress. They might also result in less sharing of ideas and limited researcher-access to genotypic and phenotypic data, and this again could eventually result in less genetic progress.

In centralised breeding programmes, the involvement of farmers could also be reduced, especially if breeding is performed in-house and if selection occurs early. Farmer involvement is useful both because it helps to identify problems and errors in genetic evaluations that affect specific animals, and because their reduced involvement in selection decisions may make farmers less accountable for the welfare of their animals. If private farmers continue to influence selection and mating decisions in the breeding programme, it is desirable that they should have some knowledge of, or at least confidence in, the breeding values, because this will make them more likely to use breeding values in their own decision-making instead of non-objective information such as show results. Here, it is a problem that genomic breeding values are probably more difficult to explain to some farmers than traditional breeding values.

Possible future decay in accuracy of genomic BV

Presently, many bulls are progeny-tested each year, and unbiased breeding values (or related measures) are available as response variables for genomic predictions. However, this situation may soon worsen as genomic breeding schemes are implemented. If increased competition and a focus on short-term benefits result in fewer bulls being used, the number of relevant animals in the reference population and the accuracy of genomic BV will decrease. High selection intensity of bulls results in a low number of bulls in the reference population, so a balance between these two factors must be found. An appropriate balance for production traits may yield too small a reference population for welfare traits characterised by lower heritability. Also, breeding organisations may choose to save immediate costs associated with genotyping or the recording of phenotypes at the expense of long-term genetic progress, especially where welfare traits are concerned.

The accuracy of genomic BV decreases with an increasing generation lag between selection candidates and animals in the reference population. Thus, marker effects need to be re-estimated frequently. Lack of resources (eg financial, change of personnel) may result in estimates being updated less frequently than is desirable, as has often happened with genetic parameters in traditional evaluations. This could result in more unfavourable mutations accumulating, in desirable gene-interactions becoming lost, and so on. This risk is probably higher for numerically small breeds and countries. Also, appropriate statistical models are sometimes developed for a large population (eg breed or country) and applied without careful tests in smaller populations. This may be problematic, because little is known about how the robustness of statistical models for genomic analysis compares with traditional BLUP models (Henderson 1984). The latter rely on fewer assumptions and are quite robust.

Today, genomic selection is implemented without optimising long-term response. Although it is superior in the short-term, genomic selection is likely to lead to a more rapid decline in genetic variance and thereby offer fewer opportunities for long-term genetic response than traditional selection unless methods to maximise long-term genetic contributions are implemented (Goddard 2009). This requires favourable alleles with low frequency to be given greater selection emphasis. Quite often, however, no estimates are available for such alleles, because information about them was discarded when marker effects were estimated or is not yet available.

The variance of genetic progress increases when bulls are selected with lower accuracy. Thus, genomic selection could be more risky than traditional selection based on progeny group-testing. However, less inbreeding and reduced drift variance with genomic selection could more than compensate for this.

A minor concern: necessary blood sampling or hair pulling may cause stress

Currently, blood samples or pulled hair roots are taken from selection candidates and animals in the reference population for genotyping. This is associated with a short period of stress for each animal. In Denmark and Sweden, blood samples will be taken from 1,200 young bulls and 600 females this year, but the number is expected to increase. DNA testing is based on hair roots in some countries (eg the US) because it is easier for farmers to pull out hair than it is to arrange for a blood sample to be taken. However, the hair root method is probably no less stressful to the animal than the taking of a blood sample. Efforts to use a fraction of the animal's ear, retrieved during ear-tagging, for genotyping are being pursued and may improve animal welfare.

Animal welfare implications

Genomic selection is here and here to stay. Its potential to improve genetic progress in general and the genetic basis of animal welfare in particular is considerable. However, there are also some grave risks. Breeders ought to use conservative breeding schemes until the long-term effects of rapid schemes have been investigated further. Such investigations should incorporate realistic effects of mutations.

In practice, this may not happen. Breeding schemes with very low generation intervals can yield the most genetic progress for evaluated traits per year even though they carry a higher risk of unwanted side-effects resulting in increased welfare problems. The recording and genetic evaluation of welfare traits is crucial if genetic deterioration in animal welfare is to be avoided. Most of the advantages listed above rely on phenotypic records being available for welfare traits. However, such records are not available in most current dairy cattle breeding programmes.

To allow breeding companies to take care of things on their own is probably inadvisable, because strong competition between breeding organisations is likely to lead to decisions that seem economically attractive in the short term but could damage the welfare of cows in the long term. Equally, so far at least, legislation has not been able to deal effectively with the animal welfare problems caused by short-sighted, economically-motivated breeding goals (Olsson *et al* 2006).

In view of these concerns, it appears that it will be necessary to mobilise a wide range of stakeholders to monitor developments and keep up the pressure on breeding companies. In this way, the companies will ideally be encouraged to see the need to take precautionary measures to avoid negative effects on animal welfare and to invest in breeding for better animal welfare. Publically funded research in the area of farm animal breeding confers a major responsibility on those involved to monitor developments and make any findings available both to the scientific community and to a wider public, including the farming community. It is also important for farmers' organisations and the extension service to engage in the debate about proper farm animal breeding. Clearly, animal welfare organisations and various national and international advisory bodies in the area of animal welfare will also have a vital role to play. Last, but not least, large food producers and retailers ought to demand high levels of farm animal welfare in all parts of the foodchain — including schemes for farm animal breeding.

Acknowledgements

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